Mites as biological tags of their hosts

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Abstract

Movements and spatial distribution of host populations are expected to shape the genetic structure of their parasite populations. Comparing the genetic patterns of both interacting species may improve our understanding of their evolutionary history. Moreover, genetic analyses of parasites with horizontal transmission may serve as indicators of historical events or current demographic processes that are not apparent in the genetic signature of their hosts. Here, we compared mitochondrial variation in populations of the ectoparasitic mite Spinturnix myoti with the genetic pattern of its host, the Maghrebian bat Myotis punicus in North Africa and in the islands of Corsica and Sardinia. Mite mitochondrial differentiation among populations was correlated with both host mitochondrial and nuclear differentiation, suggesting spatial co-differentiation of the lineages of the two interacting species. Therefore our results suggest that parasite dispersal is exclusively mediated by host movements, with open water between landmasses as a main barrier for host and parasite dispersal. Surprisingly the unique presence of a continental European mite lineage in Corsica was inconsistent with host phylogeographical history and strongly suggests the former presence of European mouse-eared bats on this island. Parasites may thus act as biological tags to reveal the presence of their now locally extinct host.

Keywords: Corsica, mtDNA, North Africa, population genetics, Sardinia, Spinturnicidae

Received 9 February 2010; revision received 21 April 2010; accepted 27 April 2010

Introduction

Comparative phylogeographical studies can expand our understanding of the ecology and evolutionary history of host and parasite populations (Nieberding & Olivieri 2007). For parasites, hosts represent a patchy and dynamic resource that varies spatially and temporally. At the population level, demography, movements and distribution of hosts are the main factors determining genetic structure of parasite populations, especially for parasites without free-living stages or with low dispersal ability (Nadler 1995; Criscione et al. 2005; Huyse et al. 2005; Whiteman & Parker 2005; Barrett et al. 2008; McCoy 2009; Biollaz et al. 2010). Although evidence for vertical transmission is difficult to ascertain (see e.g. Schwarz et al. 2008), vertically transmitted parasites are assumed to best retain the genealogical history of their host (Rannala & Michalakis 2003; Wirth et al. 2005). However, horizontally transmitted parasites can also provide information on ecological history of their hosts by revealing non-reproductive interactions (Criscione & Blouin 2004; Whiteman et al. 2004). The population genetics of such parasites could serve as indicators of historical events or current demographic processes that are not apparent in the genetic signature of their hosts. For example, Reed et al. (2004) have used parasite genealogies to infer direct contact between modern and archaic humans.

The aims of this study were to assess the phylogeographic pattern of one parasite species, to investigate how constraints imposed by the host’s spatial distribution influence parasite genetic structure and to evaluate whether parasites may be used as biological tags of their hosts. As a model system, we used the wing mite Spinturnix myoti parasitizing three closely related bat
species in the Western Palearctic region: the Maghrebian bat, *Myotis punicus*, the greater and the lesser mouse-eared bats, *M. myotis* and *M. blythii*. Bats are flying and nocturnal mammals with cryptic lifestyles and the survey of their parasites may give more insight into their ecology and evolutionary history. Spinturnicid mite are ectoparasites living exclusively on the wing membranes of their bat hosts (Deunff & Beaucournu 1981). They are direct (no intermediate host), obligate (no free-living stage) and contact transmitted parasites that cannot survive separately from their host for more than a few hours (Giorgi et al. 2004). As these mites depend strictly on host body contact for dispersal, they are especially suitable for inferring the history and ecology of their hosts. Unlike in other mammal host-parasite systems, adult female bats are more heavily parasitized than males (Zahn & Rupp 2004; Lucan 2006; Christe et al. 2007). Female bat aggregation within breeding colonies (facilitating vertical and horizontal transmission) combined with a decrease in immune defences during pregnancy may constitute optimal conditions for parasite reproduction (Christe et al. 2000). Indeed, several studies showed that *Spinturnix* synchronize their reproduction with that of their hosts, with an increase in both prevalence and intensity during the reproductive period (Christe et al. 2000; Lucan 2006; Lourenco & Palmeirim 2007, 2008; Reckardt & Kerth 2009). Prevalence and intensity are lower on individual bats during spring and autumn and their reproductive activity is greatly reduced during hibernation (Rudnick 1960; Deunff & Beaucournu 1981; Lourenco & Palmeirim 2007, 2008). The precise generation time of *Spinturnix* is still not known but much shorter than that of its host.

The prevalence of *Spinturnix myoti* reaches almost 100% during summer in the three bat species (Christe et al. 2000; pers. obs.). The average intensity on adult females is about 7, 10 and 15 mites for *M. blythii*, *M. myotis* and *M. punicus* respectively (Christe et al. 2000, 2003, 2007; *M. punicus*: this study, unpublished). According to Bruyndonckx et al. (2009a), different *Spinturnix* species are never found on the same individual bat. Moreover, phylogenetic reconstruction of bat hosts and wing mites showed evidence for cospeciation and suggested that their evolutionary history involved also failure to speciate events and host switches (Bruyndonckx et al. 2009a).

The Maghrebian bat is widespread over western North Africa and also occurs on three Mediterranean islands (i.e. Corsica, Sardinia and Malta: Castella et al. 2000; Topál & Ruedi 2001; Biollaz et al. 2010). The greater and lesser mouse-eared bats are living in sympatry throughout Western Europe and the Near East (Arlettaz et al. 1997b; Ruedi et al. 2008) and have never been found in sympatry with the Maghrebian bat. Here we focused on the association between *S. myoti* and *M. punicus* and collected mites over most of the distribution range of the host (Fig. 1). A recent genetic survey showed that island colonization by the Maghrebian bats has certainly occurred in a stepping stone manner during the Pleistocene, with currently hardly any gene flow between Corsica, Sardinia and North Africa (Biollaz et al. 2010). In contrast, within landmasses both males and females seem to be strong dispersers, even if in North Africa females appeared to be more philopat-

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**Fig. 1** Map of the studied area showing the 11 sampled populations of *S. myoti* on *M. punicus* (black stars) and five locations of additional mite samples from *M. myotis* and *M. blythii* (white stars). Distribution range of *M. punicus* is in dark grey and that of *M. myotis* and *blythii* in light grey. Arrows represent potential colonization routes of the islands of Corsica and Sardinia by the wing mite *S. myoti*.

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ric than males (Biollaz et al. 2010). Based on our know-
ledge of the host and the life style of the parasite, we
expect mitcline genetic patterns to reflect that of its host i.e.
more population differentiation between landmasses
than within landmasses. Moreover, if mites followed
their hosts in the colonization processes, we expect a
lower genetic diversity in insular populations.

Methods

Sampling

In spring and summer 2006, we collected mites in 11
colonies of M. puniceus in North Africa, Corsica and Sardinia
covering most of the known distribution area of the host
(Fig. 1). Most nursery colonies were composed of adult
females and a few males living in natural caves or aban-
doned mines. To avoid disturbance during lactation, bats
were caught before or at the end of the breeding season
directly inside the nursery colonies during the day or
mist-netted at the entrance of the cave at night. Animals
were kept in separate textile bags to avoid contamination
between individuals. Mites were collected with soft for-
ceps from the bat wing membranes and preserved in
ethanol 90% until processing. Five to seven mites per
colony, each from a distinct bat, were used for the
genetic analyses. As S. myoti is present on three host
species, we added in the phylogenetic analysis some
S. myoti samples of M. myotis and M. blythii from five
colonies in Spain, Switzerland and Italy (Fig. 1).

Mite DNA amplification and analyses

DNA was extracted from each mite using a standard
proteinase K-phenol chloroform method (Sambrook
et al. 1989). We amplified and sequenced the 16S rRNA
gene (16S) and the cytochrome oxydase subunit I (COI)
as described in Bruyndonckx et al. (2009a). All products
were analysed on an ABI Prism 3100 genetic analyzer
(Applied Biosystems). Mite sequences were aligned and
edited with SEQUENCE NAVIGATOR (Parker 1997).

We used ARLEQUIN 3.1 (Excoffier et al. 2005) to assess
the number of haplotypes (N), haplotype diversity (h)
and nucleotide diversity (π) within each population.
Mean uncorrected genetic p-distances between colonies
within and among landmasses (Corsica, Sardinia and
North Africa) were calculated with MEGA 3.1 (Kumar
et al. 2004). We constructed the haplotype network using
the method of statistical parsimony implemented in the
software TCS 1.21 (Clement et al. 2000). Evolutionary
relationships among all haplotypes of S. myoti populations
were estimated by constructing phylogenetic trees using
Bayesian and maximum-likelihood (ML) analyses. The
Bayesian analysis was carried out using MrBayes 3.1
(Huelsenbeck et al. 2001), based on the most appropriate
models of DNA substitution determined using MrMod-
deltest 2.2 (Nylander 2004). This model (hLRT criterion)
was a GTR + I + G (Rodriguez et al. 1990; Yang 1994).
The Markov chain was run for 5 000 000 generations and
sampled once every 1000 generations; burn-in was set to
the first 1500 trees. To ensure convergence in the Bay-
esian analysis, two independent runs were performed.
The ML analysis was performed with PhyML 3.0 software
(Guindon & Gascuel 2003), with the same parameters for
the substitution model as suggested by MrModeltest 2.2.
We generated bootstrap values based on 1000 resampled
data sets. The trees were rooted using two specimens of a
closely related species of the same genus, S. anegavinas
(EU784873–EU784927 and EU784874–EU784928).

A hierarchical analysis of molecular variance (AMOVA)
(Excoffier et al. 1992), inferred with ARLEQUIN 3.1 (Exco-
fier et al. 2005), was used to estimate Φ-statistics which
incorporate information on nucleotide differences
between haplotypes. Hence the proportions of variation
among landmasses (Φlandmass-total), between colonies
within landmasses (Φcolonies-landmass) and within colonies
(Φindividuals-colonies) were estimated. The significance
of these Φ-statistic values was assessed through random-
izations using 10 000 permutations. We calculated
pairwise Φ-statistics among all colonies with the same
software. To test whether Φ-statistics are sensitive to
distances between haplotypes, we performed the same
analyses based only on haplotypic frequencies.

We used BEAST v.1.4.8 (Drummond & Rambaut 2007)
infer the time to the most recent common ancestor
(TMRCA) of Sardinian populations. Because Coriscan
populations shared their unique haplotype with a Spa-
nish population, it was not possible to infer the TMRCA
of Corsican populations. We specified a relaxed clock
with an uncorrelated lognormal distribution (Drum-
mond et al. 2006) and a speciation Yule process as the
tree prior. The rate of molecular evolution in Spinturni-
cid mites is unknown, as such we specified a prior distri-
bution on evolutionary rate (1.3 ± 0.3%/Myr) on the
basis of the pairwise 16S and CO mutation rates of
Arthropods (Brower 1994) and of the Orders Opiliones
and Scorpiones (Gantenbein & Bargiader 2003; Thomas
& Hedin 2008; Ben Othmen et al. 2009). We performed
two independent runs of 10 000 000 generations sam-
ping every 1000 steps and removing 10% of the initial
samples as burn-in. To control for convergence and to
visualize the results, we used the program TRACER v.1.4
(Drummond & Rambaut 2007).

Host and parasite comparison

Host mitochondrial and nuclear Fst values were
obtained from Biollaz et al. (2010), which included indi-

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individual hosts of parasites sequenced in the present study. We calculated mite pairwise $F_{ST_{mite}}$ based on haplotypic frequencies only and tested the correlation between mite and host $F_{ST_{mite}}$ and between mite $F_{ST_{mite}}$ and host $F_{ST_{nuc}}$, all measured as $F_{ST}/(1 - F_{ST})$. To determine if parasites were tracking host inter-colony gene flow, we used a Mantel test in FSTAT 2.9.4 (Goudet 2002) to test the correlation between ectoparasite and host genetic distances. The colony of Masainas (Sardinia) was removed due to low host sample size.

**Results**

*Mite genetic analyses*

Among the 58 *S. myoti* associated with *M. punicus* sequenced, 21 different 16S/COI haplotypes were detected (one in Corsica, nine in Sardinia and 11 in North Africa, Table 1). The 963 aligned nucleotides consisted of 42 variable sites of which 32 were parsimony-informative. 165 and COI haplotypes were deposited in GenBank under accession numbers FJ225940–961 and FJ225883–904, respectively. A detailed list of the sampling localities, number of mites analysed per colony and mtDNA haplotypes per population are provided in Table 1.

The Bayesian and ML consensus trees (Fig. 2) revealed three well-supported clades corresponding to the same geographical groups defined by the haplotype network (Fig. 3). Unlike host phylogenetic pattern (Fig. 4), the first parasite clade covered Corsica and continental Europe with the same haplotype (c1) present all over Corsica and in Spain (Table 1, Figs. 2 and 3). The second clade comprised the North African populations and the last one the Sardinian populations (Figs. 2–4). We found no shared haplotypes between those three regions (Figs. 2 and 3). The uncorrected genetic $p$-distances were 1.5% between Corsica and Sardinia, 2.0% between Corsica and North Africa and finally 2.5% between Sardinia and North Africa. The percentage of divergence within Corsica was null, 0.002% within Sardinia and 0.003% within North Africa. The haplotype number per population ranged from 1 to 6 (mean = 2.9, Table 1). Haplotype diversity ranged from 0.0 to 1.0 (mean = 0.587, Table 1) and nucleotide diversity (%) from 0.0 to 0.402 (mean = 0.152; Table 1). Genetic diversity indices ($N, h, \pi$) were higher in North African populations than in Sardinian populations, which in turn were higher than Corsican populations.

In agreement with the heterogeneity of haplotype distribution, the hierarchical *amova* showed an important differentiation between landmasses ($\Phi_{landmass-total} = 0.91, P < 0.001$; Table 2), whereas populations within landmasses where not significantly differentiated ($\Phi_{colonies-landmass} = 0.10, P = 0.072$; Table 2). When

<table>
<thead>
<tr>
<th>Locality</th>
<th>Roost</th>
<th>Host species</th>
<th>n</th>
<th>N</th>
<th>H</th>
<th>$\pi$%</th>
<th>Haplotypic (no of individuals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corsica</td>
<td>Castifau</td>
<td>Mine</td>
<td><em>M. punicus</em></td>
<td>5</td>
<td>1</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Oletta</td>
<td>Cave</td>
<td><em>M. punicus</em></td>
<td>5</td>
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<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Casaglione</td>
<td>Building</td>
<td><em>M. punicus</em></td>
<td>5</td>
<td>1</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>Sardinia</td>
<td>Casteldoria</td>
<td>Mine</td>
<td><em>M. punicus</em></td>
<td>5</td>
<td>3</td>
<td>0.7</td>
<td>0.229</td>
</tr>
<tr>
<td></td>
<td>Borutta</td>
<td>Cave</td>
<td><em>M. punicus</em></td>
<td>5</td>
<td>3</td>
<td>0.7</td>
<td>0.229</td>
</tr>
<tr>
<td></td>
<td>Laerru</td>
<td>Cave</td>
<td><em>M. punicus</em></td>
<td>5</td>
<td>3</td>
<td>0.8</td>
<td>0.229</td>
</tr>
<tr>
<td></td>
<td>Macomer</td>
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<td><em>M. punicus</em></td>
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<td>3</td>
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</tr>
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<td><em>M. punicus</em></td>
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<td>3</td>
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<td>0.145</td>
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<td></td>
<td>1</td>
<td>0.0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Tun.</td>
<td>Cap Bon</td>
<td>Cave</td>
<td><em>M. punicus</em></td>
<td>6</td>
<td>6</td>
<td>1.0</td>
<td>0.402</td>
</tr>
<tr>
<td>Moro.</td>
<td>Wintimdoine</td>
<td>Cave</td>
<td><em>M. punicus</em></td>
<td>5</td>
<td>4</td>
<td>0.9</td>
<td>0.125</td>
</tr>
<tr>
<td></td>
<td>Ilriouado</td>
<td>Cave</td>
<td><em>M. punicus</em></td>
<td>7</td>
<td>4</td>
<td>0.9</td>
<td>0.188</td>
</tr>
<tr>
<td>Cont. Europe</td>
<td>Cadiz</td>
<td>Cave</td>
<td><em>M. myotis</em></td>
<td>4</td>
<td>4</td>
<td>1.0</td>
<td>0.277</td>
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<td></td>
<td>Malaga</td>
<td>Cave</td>
<td><em>M. myotis</em></td>
<td>4</td>
<td>3</td>
<td>0.8</td>
<td>0.156</td>
</tr>
<tr>
<td></td>
<td>Aglié</td>
<td>Building</td>
<td><em>M. myotis</em></td>
<td>3</td>
<td>3</td>
<td>1.0</td>
<td>0.277</td>
</tr>
<tr>
<td></td>
<td>Naters</td>
<td>Attic</td>
<td><em>M. myotis/lythii</em></td>
<td>2</td>
<td>4</td>
<td>0.4</td>
<td>0.360</td>
</tr>
<tr>
<td></td>
<td>Satigny</td>
<td>Attic</td>
<td><em>M. myotis</em></td>
<td>1</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

The following parameters were estimated: number of individuals sequenced per colony ($n$), total number of haplotypes ($N$), haplotype diversity ($H$), nucleotide diversity ($\pi$) and distribution of haplotypes among populations. Numbers in bracket indicate the number of individuals per haplotype. Numbers in bold indicate haplotypes that are shared between two or more localities.

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samples from continental Europe were included, populations between and within landmasses were significantly differentiated ($\Phi_{\text{landmass-total}} = 0.86, P < 0.001$; $\Phi_{\text{colonies-landmass}} = 0.19, P = 0.002$; Table 2), reflecting the high diversity on continental Europe. Those patterns were confirmed by pairwise $\Phi_{ST}$ values (Table 2): comparisons between pairs of colonies from different landmasses were all significant, except Corsican populations that were similar to a Spanish one (Malaga), while none were significant within landmasses, except the Sardinian most southern population (Masainas), which was slightly different from the most northern one (Casteldoria). Patterns of differentiation between colonies were similar but less marked when genetic distances were based only on haplotypic frequencies.

The result of the analysis with Beast suggested that the most recent common ancestor (MRCA) of Sardinian populations dates back to the Mid Pleistocene (mean: 0.354Ma, 95% HPD: 0.127–0.669Ma). This result is in accordance with that of its host, which was estimated to date back to the Early-Mid Pleistocene (Biollaz et al. 2010). However, this dating should be taken with cautious as regards no mutation rate of closely related parasitic mites is known.

**Host and parasite comparison**

We applied simple Mantel test analyses to examine the correlations among genetic distances of the host and the parasite. Mantel test analyses revealed that mite inter-population $F_{ST \text{ mito}}$ values were highly correlated with their host genetic values. This correlation was more pronounced with host $F_{ST \text{ mito}}$ than with host $F_{ST \text{ nucl}}$ values ($r = 0.763, P < 0.001$; $r = 0.508, P = 0.002$, respectively). This correlation mainly reflected the population distribution over the different landmasses, as revealed by a statistically non-significant correlation when landmasses are taken into account in the analysis.

**Discussion**

This study suggests that *S. myoti* and its host, the Maghrebian bat, share a common genetic and geographic structure. As expected, mite populations of Corsica, Sardinia and North Africa were highly differentiated with no shared haplotypes. Mite dispersal across water is currently totally hampered reflecting the bat genetic pattern (Biollaz et al. 2010). Moreover, mites seemed to
have followed their bat hosts in the island colonization process and colonized the island of Sardinia during the Pleistocene. However, one notable exception, decreasing the similarity between host and parasite patterns, is the colonization of the island of Corsica: Corsican parasites originate from continental Europe whereas their hosts have a North African origin.

Maghrebian bats from Corsica, despite their close phylogenetic relationship with those of Sardinia (Biollaz et al. 2010), harbour mites genetically similar to those infesting M. myotis/blythii from continental Europe. As mites cannot survive more than a couple of hours without their host (Giorgi et al. 2004), the presence of this continental European mite lineage on the island of Corsica is best explained by a direct switch from M. myotis/blythii to M. punicus. However, M. punicus currently does not occur in sympathy with M. myotis nor with M. blythii. The best explanation to elucidate the presence of continental European mites on Corsican bats is therefore the occurrence of mouse-eared bats on Corsica once in the past. Competitive exclusion may explain the nowadays unique presence of Maghrebian bats in Corsica, as its ecological niche is similar to that of mouse-eared bats (Arlettaz et al. 1997a; b; Castella et al. 2000).

The presence of one unique mite haplotype in Corsica might result from two successive bottlenecks: the first one when mouse-eared bats colonized Corsica from continental Europe, potentially during the Pleistocene variation of the sea level and the second one during our hypothesized host switch between the mouse-eared bat and Maghrebian bat when they co-occurred in Corsica. Competitive exclusion may also explain the nowadays absence of Sardinian mite lineages in Corsica. Only experimental survival tests of different parasite lineages in competition on the same host might permit to test this hypothesis.

The time of the most common ancestor of the Sardinian populations of S. myotis was estimated to date back

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Table 2 Hierarchical AMOVA among (A) eleven populations of Spinturnix myoti partitioned by geographical landmasses (North Africa, Sardinia, Corsica), (B) including four populations from continental Europe. Asterisks indicate significant P values

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Sum of squares</th>
<th>Variance components</th>
<th>% of variation</th>
<th>ΦST</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Among landmasses</td>
<td>2</td>
<td>337.1</td>
<td>8.86466</td>
<td>91.3</td>
<td>0.91***</td>
</tr>
<tr>
<td>Among colonies within landmasses</td>
<td>8</td>
<td>9.5</td>
<td>0.08105</td>
<td>0.83</td>
<td>0.10</td>
</tr>
<tr>
<td>Within colonies</td>
<td>47</td>
<td>35.9</td>
<td>0.76373</td>
<td>7.87</td>
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</tr>
<tr>
<td>Total</td>
<td>57</td>
<td>382.5</td>
<td>9.70943</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(B) Among landmasses</td>
<td>3</td>
<td>388.4</td>
<td>6.89100</td>
<td>86.2</td>
<td>0.86***</td>
</tr>
<tr>
<td>Among colonies within landmasses</td>
<td>11</td>
<td>21.3</td>
<td>0.21208</td>
<td>2.65</td>
<td>0.19**</td>
</tr>
<tr>
<td>Within colonies</td>
<td>60</td>
<td>53.5</td>
<td>0.89131</td>
<td>11.15</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>74</td>
<td>463.2</td>
<td>7.99439</td>
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Fig. 4 Graphical display of parasite (left side) and host (right side) bayesian consensus trees. The links represent the association between host and parasite clades.

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to the Mid Pleistocene, suggesting that mites have followed the Maghrebian bat in Sardinia. Indeed, Biollaz et al. (2010) showed that Sardinia and Corsica colonization by the Maghrebian bat might have occurred in a stepping stone manner during the Pleistocene. The emergence of land bridges due to the low sea level during the successive glacial periods favoured first the colonization of Sardinia and then the colonization of Corsica from Sardinia. The expected and observed lower haplotype and nucleotide diversity in Sardinian mites compared to North African mainland may thus result from a strong bottleneck during the colonization events (Frankham 1996). This ‘island syndrome’ has been poorly investigated in parasite species but has been reported in the nematode *Heligmosomoides polygyrus* infesting *Apodemus sylvaticus* and *Mus musculus* (Niebergding et al. 2006). Finally, the presence of the same mite haplotype in Corsica and Spain prevents the dating of the most common ancestor of Corsican populations.

Alternative hypotheses to explain the presence of a continental European mite lineage in Corsica would require the presence of the parasite *S. myoti* on other bat species inhabiting Corsica. This latter scenario would imply two host-switches and seems unlikely since we found that co-roosting bat species harboured their own specific *Spinturnix* species (more than 10% of divergence) in Corsica (Bruyndonckx et al. 2009a). A very recent colonization from the mainland seems also unlikely since the minimal distance between Corsica and Italy is approximately 80 km, a distance much larger than the strait of Bonifacio (12 km) that has been shown to represent a strong barrier to gene flow between Corsica and Sardinia for the Maghrebian bats (Biollaz et al. 2010). Other alternatives would require improbable scenarios of colonization, recolonization and extinction in Europe and Corsica.

*Spinturnix myoti* exhibited an important and significant population genetic structure between Corsica, Sardinia and North Africa, while within those three regions populations were not genetically differentiated. This latter result is consistent with a very high gene flow among mite populations within landmasses, a pattern that differs from the genetic structure of bats in North Africa (Biollaz et al. 2010). Indeed, the Maghrebian bats showed a male-biased dispersal, with females being highly philopatric, resulting in a high mitochondrial differentiation between Tunisian and Moroccan colonies (Biollaz et al. 2010). Mite dispersal among remote colonies may occur via males and females during mating where territorial males may form loose licks (Horáček & Gaisler 1986). Parasite transmission during mating has been recently suggested to strongly influence population genetics in the mite *Spinturnix* infesting the Bechstein’s bat (*Myotis bechsteinii*) (Bruyndonckx et al. 2009b). Moreover, in North Africa, bats have been reported to hibernate from time to time in small clusters which could give opportunities for mite dispersal (Kowalski et al. 1986). A detailed picture of mite movements can be revealed in the future through the use of microsatellite markers which development is currently in progress. Other studies on the importance of host movements on the genetic structure of parasite populations have been previously documented, for example in nematodes of Ungulates (Blouin et al. 1995), in trematodes that infect salmonid fishes (Criscione & Blouin 2004) and in seabird ticks (McCoy et al. 2003).
In addition to their use in detecting cryptic species (Criscone & Blouin 2004), refuges during glaciations (Nieberding et al. 2004; Toon & Hughes 2008), former contacts (Reed et al. 2004) and demography (Biek et al. 2006) of their hosts, we show that a parasite with both vertical and horizontal transmission might also reveal the past co-occurrence and contact of different host species that allowed the exchange of parasite lineages. The past distribution of presently extinct populations of host plants was similarly highlighted by the genetic pattern of its symbiont (Anderson et al. 2004). In conclusion, the population structure of S. myoti is highly dependent on host movements. This contact transmitted parasite appears to be a good proxy to detect the former presence of a nowadays locally extinct host species, i.e. mouse-eared bats in Corsica, that would have been virtually impossible to reveal without good fossil evidence.

Acknowledgements

We are grateful to many people who assisted with the collection of specimens especially G. Beuneux (Groupe Chiroptères Corse), C. Ibáñez, J. Quetglas, A. Popa-Lisseanu, J. Juste (Estación Biológica de Doñana, Sevilla), J. Ramon and Olivido (Malaga), M. Mucceda (Sardinia), Chef de la brigade de chasse de Nabeul (Tunisia), L. Faouzi, A. Ighous (Morocco), E. Patriarca, P. Debernardi (Italy), R. Arlettaz, P. Roduit (Suisse). Thanks to G. Devevey, G. Emarosi, P. Fontanillas, A. Horn, Ana Popa-Lisseanu, L. Keller, 3 anonymous referees and F. Baloux for useful comments on the manuscript and F. Witsenburg for the English revision of the manuscript. This work is supported by the Swiss National Science Foundation 31003A_120479.

References


